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# Investigating the Effect of Exercise on Working Memory Encoding, Resolution, and Maintenance

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by

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# ABSTRACT

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by

Lindsey Christine Purpura

Working memory is a fundamental cognitive ability that underlies our action and performance in daily life. Since working memory is such a critical function, it is important to understand how it may be affected by varied behavioral states. One such state is exercise. It is reasonable to expect, and it has been demonstrated in previous literature, that exercise, reflective of movement through our environment, has an impact on brain activity through altered neuronal firing patterns, the stimulation of brain derived neurotrophic factor (BDNF), and altered neurotransmitter concentrations (Bullock, Elliot, Serences, & Giesbrecht, 2017; Hakansson et al., 2016; McMorris, Sproule, Turner, & Hale, 2010). The current study aims to elucidate the effect of exercise on working memory encoding, resolution, and maintenance. Previous research provides mixed findings regarding the effect of exercise on working memory, which suggest that separating the components of working memory is critical to understanding this effect. The current studies employ two working memory paradigms that allow us to critically investigate encoding and resolution (study 1) as well as maintenance and encoding efficiency (study 2). The results from study one suggest that encoding rates

decrease for larger set sizes during exercise compared to at rest and, subsequently, the resolution of encoded information is higher during exercise compared to at rest. Results from study two suggest that low capacity subjects encode less information from supra-capacity arrays during exercise, however, this result should be interpreted cautiously. While these data do not provide a clear picture of the effect of exercise on working memory, we do see clear evidence that low intensity exercise modulates working memory in some way. Further research is needed to elucidate and explore the neural mechanisms of these effects.

**Effect of exercise on working memory**

Working memory (WM) is a fundamental cognitive process that mediates our ability to maintain and manipulate information necessary for current task goals. Without our conscious knowledge, we employ WM almost constantly in our daily lives to keep information "on-line" for our goal-directed behavior. It is essential for coherent and adaptive human behavior in everyday life and as such, it must function efficiently under varied conditions and behavioral states.

Since the unconscious nature of our use of WM may limit our ability to truly understand it's importance in our daily life, thinking of WM as a component and application of executive function may help. Executive function is a broad term that captures cognitive functions including: working memory, attentional control, inhibitory control, cognitive flexibility, planning, and more. Imagining deficits that may result as a product of impaired executive functioning is simple. Without proper executive control you may experience cognitive symptoms including difficulty paying attention, increased distractibility, and poor maintenance of information; these may manifest behaviorally as poor listening, inappropriate behavior, and difficulty following instructions. Unsurprisingly, research in children reveals that working memory deficits, typically denoted as having low capacity, can lead to marked learning impairments (Alloway, Gathercole, & Elliot, 2010; Gathercole & Pickering, 2000). Alarmingly, students who demonstrate deficits in working memory perform similarly to those clinically diagnosed with ADHD on both verbal and visuospatial WM tasks and a teacher assessment of classroom behaviors related to WM deficits (Alloway, Gathercole, & Elliot, 2010). These data suggest that learning impairments may be present even in those children without a clinical diagnosis who suffer from low WM capacity.

It can be argued that three subcomponents of executive control (attentional control, inhibitory control, and WM) are tightly intertwined. In fact, recent research suggests that a key difference between low and high WM capacity individuals is their ability to filter out irrelevant information from to-be-encoded information (Vogel, McCullough, & Machizawa, 2005). These data suggest, then, that WM may be thought of as the distribution of attention to relevant bits of information (attentional control), inhibition of irrelevant bits of information (inhibitory control), and maintenance of the encoded information. If this is the case, understanding WM is more than just testing ability to remember small bits of information over short retention intervals, but rather, we must understand how information is encoded, how this happens efficiently, and what behavioral states affect which stages of these processes.

Considering the fundamental nature of WM, it is important to ask what may affect WM encoding and maintenance. One of the most pronounced influences on WM capacity is age; it is widely accepted that WM capacity is one of various cognitive functions that declines with age. It is critical to understand, though, if this decline is due to a limitation in resources available for the retention of information or due to an altered ability to efficiently encode information. There is mounting evidence for the latter. Data from an fMRI study comparing younger and older adults demonstrated decreased suppression of brain activity to irrelevant information in older compared to younger adults (Gazzaley, Cooney, Rissman, & D'Esposito, 2005). Participants were instructed to attend to a stream of images that contained both faces and scenes. Critically, however, participants were instructed at the beginning of each block to attend to faces, scenes, or to passively observe all images. The researchers were particularly interested in BOLD activation patterns in the left parahippocampal/lingual gyrus, a scene selective ROI. Data indicated similar enhancement of information in younger and older adults such that the activation patterns in the ROI were similar in the two age groups when instructed to attend to scenes compared to passive viewing. Interestingly, though, 88% of younger adults showed suppressed BOLD activation in the ROI during ignore scene compared to passive view blocks while only 44% of older adults showed this suppression effect. Suppression indexes (BOLD activation for passive view minus BOLD activation for ignore scene blocks) were correlated with WM performance. Critically, the researchers showed that those older adults who showed similar suppression to the younger adults had intact WM performance (Gazzaley, Cooney, Rissman, & D'Esposito, 2005). These data strongly support the notion that suppression, or inhibitory control, is a key factor and, perhaps, determinant, of WM performance.

Further research in older adults using EEG data from a filtering task showed similar results; older adults were less efficient at filtering information compared to younger adults (Schwarzkopp, Mayr, & Jost, 2016). The use of EEG data allowed for a more critical assessment of the time-course of this effect and results showed that this effect emerged early in retention but disappeared by the end of the prescribed retention interval. The researchers interpreted this to suggest that older adults may not filter, or inhibit, irrelevant information as readily as younger adults during encoding. However, they may employ a late selection filtering system as a compensatory mechanism whereby the irrelevant information is filtered out at a later stage in older adults compared to younger adults (Schwarzkopp, Mayr, & Jost, 2016). While this late stage filtering process may be sufficient when the combined relevant and irrelevant information is within capacity, impaired performance may be observed when the sum of relevant and irrelevant information is above capacity. In this case, inefficient filtering of irrelevant information during encoding may result in insufficient encoding of relevant information. These findings suggest that declines in WM associated with age may be related to encoding efficiency rather than available resources.

Due to the abundance of research concerning WM performance in humans, various paradigms exist to measure and assess WM performance. Two paradigms, in particular, allow for the critical assessment of encoding performance.

First, the continuous response modeling paradigm uses a basic WM single target probe paradigm but with a continuous response rather than a 2-alternative forced choice model (Zhang & Luck, 2008). In this paradigm, the participant first sees an array of colored squares and is then probed to report the color of one single item. This response is reported by selecting a color on a color wheel that most closely matches the remembered color. From these data, an error score can be calculated as the distance (in degrees) from the correct color to the reported color. This paradigm allows for testing various set sizes and enables the researcher to model error rates in order to estimate two key parameters: probability in memory (Pmem) and resolution (Zhang & Luck, 2008). Probability in memory is estimated based on a participant's distribution of responses and is the likelihood, based on said distribution, that a given error score occurred due to resolution variability or due to guessing (indicating that the probed item was not present in WM at test). Simply stated, Pmem estimates whether the item was in or out of memory. Resolution represents the clarity of the encoded representation. This parameter is estimated for trials that are categorized as "in-memory" based on the distribution of errors and may be operationalized as the standard deviation of error rates. Simply stated, resolution represents the average error in reporting when the probed item was, in fact, encoded. These two parameters, Pmem and resolution, can be compared for different set sizes to understand how the likelihood of encoding and resolution change with increasing set size and under varied experimental conditions.

Another way to investigate WM encoding and maintenance is to use a paradigm specifically created to elicit a lateralized ERP associated with WM referred to as contralateral delay activity (CDA). The CDA is a difference wave calculated by subtracting the ipsilateral waveform from the contralateral waveform elicited during a retention interval to a lateralized WM task. WM tasks can be lateralized by providing an endogenous cue to attend to and encode either hemifield of a sample array. During the retention interval, then, we see a negative going ERP that is more negative in the contralateral hemisphere (to the encoded hemifield) than ipsilateral. The amplitude of the CDA (the contralateral minus ipsilateral wave) tracks with the number of items encoded (Vogel, McCullough, & Machizawa, 2005). A variant of this task includes both task relevant and irrelevant items. CDA amplitude can be compared for trials with the same number of total items but different proportions of relevant and irrelevant items. This allows for an assessment of encoding and filtering efficiency.

Previous evidence from research employing lateralized WM tasks to assess the CDA show that low capacity subjects have impaired filtering compared to high capacity subjects (Vogel, McCullough, & Machizawa, 2005). This was evidenced by CDA amplitudes on trials with only two relevant items but four total items that were comparable to those for trials with four relevant items. This suggests that these low capacity subjects were encoding the irrelevant information along with the relevant items. This, again, could be an indication that WM capacity and limitations are less an issue of pure capacity but rather of encoding efficiency.

**Effect of Exercise on Working Memory**

Changes in behavioral state induced by locomotor activity dramatically impact cognitive performance and brain activity. This has been demonstrated in various species from invertebrates to nonhuman primates (Bullock, Cecotti, & Giesbrecht, 2015; Chiappe, Seelig, Reiser, & Jayaraman, 2010; Niell & Stryker, 2010; McAdams & Maunsell, 1999). As previously stated, WM is a critical cognitive function that underlies various other processes and, as such, it is important to understand how this function may be altered by behavioral state. Specifically, we are interested in understanding how exercise may affect WM performance.

There is a growing body of literature regarding the acute effects of exercise on WM (for a review, see: McMorris, Sproule, Turner, & Hale, 2010). Notably, however, findings regarding whether exercise benefits or impairs WM are mixed. Generally, there is evidence for improved reaction time on WM tasks after acute bouts of exercise (Chen, Zhu, Yan, & Yin, 2016; Kamijo et al., 2009; McMorris, Sproule, Turner, & Hale, 2010; Pontifex, Hillman, Fernhall, Thompson, & Valentini, 2008; Yanagisawa et al., 2016). Support for this effect emerges from experiments using N-back, Sternberg, Stroop tasks, and others. The fact that support for this has emerged using multiple different tasks may argue that this benefit can be applied to WM tasks that require both simple maintenance, maintenance plus updating, and inhibitory components. Conversely, there is evidence that acute bouts of moderate intensity exercise result in decreased accuracy (Dietrich & Sparling, 2004; McMorris, Sproule, Turner, & Hale, 2010). While the exact effects and neural mechanisms of these effects are not clearly defined, it seems apparent that exercise does alter performance in some way.

One critical component to clearly elucidating the effect of exercise is to critically consider task requirements. Working memory tasks range from those requiring simple maintenance, to requiring maintenance and updating, and some requiring maintenance, updating, manipulation, and inhibition. Perhaps these sub components of WM are affected differentially by exercise, thus, creating the current conflicting body of evidence. In an attempt to separate these components, Audiffren and colleagues (2009) used a random number generating task that was able to assess inhibition and updating or WM separately. Results indicated that during exercise, participants demonstrated impaired inhibition and a shift to an easier strategy.

Finally, it is important to keep in mind that exercise may be thought of as a stressor. Previous evidence has shown impaired memory performance in both rats and non-human primates through altered hippocampal activity and increased dopamine release when experience artificially and experimentally induced stress (Gamo et al., 2015; Grauer & Kapon, 1993). It is possible that the same exercise manipulation may affect participants differentially based on physical fitness, familiarity with exercise, and even task performance. This is to say that participants who are high or low performers for a certain task may present different effects of exercise if observed exercise effects are related to a stress response. Those who are high performers and familiar with exercise may experience a benefit of exercise while low performers or less comfortable participants may experience a detrimental stress reaction and decreased performance during exercise.

Due to the incongruity in the current body of literature regarding the acute effects of exercise on WM, it is difficult to make strong arguments for the true effect of exercise on WM. It is clear that further research is required to understand this relationship and to elucidate the components of WM and executive function that may be altered by exercise. The current study aims to investigate the effect of acute bouts of exercise on WM encoding, resolution, and maintenance, with additional consideration of individual WM capacity.

## Study 1

To investigate the nature of the impact of physical activity on WM encoding and resolution, the current study employed a continuous response WM task. The data were modeled using a maximum likelihood estimation procedure to determine whether changes in physical activity modulated the probability that information was encoded in memory, the quality of the encoded information, or some combination of the two (Zhang & Luck, 2008). It was hypothesized that the probability of encoding would be lower for larger (six item) arrays compared to smaller (3 item) arrays as the larger arrays would be above capacity for most subjects. Further, it was hypothesized that resolution would be greater for smaller arrays compared to larger arrays. Based on previous evidence for enhanced task performance during exercise, it was hypothesized that exercise would have a beneficial effect on performance. Enhanced performance may manifest as increased probability that an item was encoded or better resolution of encoded items. As WM capacity is generally accepted as a stable trait, enhanced performance is expected to manifest as enhanced resolution during exercise compared to rest. These benefits were specifically expected within the low intensity exercise condition compared to rest and high intensity due to previous evidence for an inverted U effect of exercise on cognition (McMorris, Sproule, Turner, & Hale, 2010).

### Method

**Participants.** Participants were 22 students from the University of California, Santa Barbara (UCSB) and 1 community member ($M_{age}$ = 20.13, $SD_{age}$ = 2.28). Participants received financial compensation for their participation ($20/hour). Five participants were excluded form all analyses due to error greater than 2.5 standard deviations above the mean in at least one condition. All participants had self-reported normal vision with no corrective lenses or contacts. Before participation, all participants completed the Physical Activity Readiness Questionnaire (PAR-Q; National Academy of Sports Medicine) to ensure eligibility to engage in aerobic activity and all participants provided informed consent. All procedures were approved by the UCSB Human Subjects Committee and the US Army Human Research Protection Office.

**Materials.**

***Stationary Bike.*** Physical activity was manipulated on a stationary bike, CycleOps 400 Pro Indoor Cycle (Saris Cycling Group, Madison, WI, USA). T2+ Profile Design Aero Bars (Profile Design, Long Beach, CA, USA) were attached to the handlebars and a Logitech Trackball Mouse (Logitech, Newark, CA, USA) was fixed to the end of the bars. The aero bars allowed the participant to rest their elbows on the bars and be hands free to complete the task using the affixed mouse. This set-up also helped to minimize upper body and head movements during task completion. A CycleOps wireless heart rate monitor was used along with Trainer Road software (Trainer Road, Reno, Nevada) to monitor heart rate.

***Astrand-Rhyming Submaximal Bike Test.*** This fitness test provides a measure of estimated maximal oxygen consumption ($VO_2$max). The test is as follows: 5-minute warm-up at a low pedaling resistance (~50 Watts (W) of power), 6-minute test phase at higher pedaling resistance (between 80 and 160W depending on individual fitness), 2-minute cool-down (50W). The goal was to elevate the subject's heart rate to a relatively stable level above 120 BPM (beats per minute) in the final two-minutes of the testing phase. Heart rate was continuously recorded and the subject's average heart rate over the last two minutes along with power output were used to calculate an estimate of absolute $VO_2max$ ($mL \bullet min^{-1}$) as guided by Astrand-Rhyming (1954). An estimate of relative $VO_2max$ ($mL \bullet kg^{-1} \bullet min^{-1}$) can be calculated by dividing absolute $VO_2max$ by the subject's body mass (kg), in accordance with ACSM guidelines (ACSM, 2007, pg. 7).

***Change Detection Working Memory Task.*** In order to obtain a baseline measure of individual WM capacity, participants completed a change detection task. The task consisted of two blocks of 48 trials each. One trial consisted of a brief sample array (100ms) followed immediately by a test screen until response (see Figure 1). The sample array was a grey screen with a central fixation and either four (two per hemifield, 50% of trials) or eight squares (three per hemifield, 50% of trials). Participants were instructed to fixate the center and retain color and location information of the squares from the brief sample array. The test screen consisted of a single probe item. Participants were to indicate, by keypress, whether the presented probe was the same or different color from the square that was in that location in the sample array. Squares in the sample and test array subtended 0.5° visual angle and items in the sample array had a minimum distance from center to center of 1.5° visual angle. Stimulus colors were selected from six distinct colors (rest, lime, blue, yellow, white, black) and never appeared more than twice within one sample array. A capacity score (K) was calculated for each subject using responses to set size eight trials and the equation: $K = 8 * (\text{hits} - \text{false alarms}) / (1 - \text{false alarms})$, where a hit is correct change detection and a false alarm is when a change is reported but no change was present.

***Continuous Response Working Memory Task.*** The continuous response WM task is a variant of similar paradigms in WM literature (Zhang & Luck, 2008). The current study employed a gaze contingent version in which participants fixate the center of the screen and initiate each trial by mouse press. Each trial consisted of a sample array of three (50% of trials) or six (50% of trials) colored squares (100ms), a retention interval (900ms), and a response display (see Figure 2). If eye position deviated >1.5° of visual angle during the presentation of the sample array or retention interval, the trial was terminated and added to the end of the block trial sequence. The squares in the sample and test arrays subtended 1° visual angle and were arranged in a circle around the fixation with a radius of 1.5° visual angle. The stimulus colors were randomly selected from 25 possible colors evenly distributed around a full spectrum color wheel. On each trial, no color within two steps in either direction on the color wheel from the color of the to-be-probed item was presented. The response screen consisted of a full spectrum color wheel with a single location probe; participants were asked to report the color of the item that was presented at the probe location by selecting the appropriate color on the wheel. The probe was the outline of a square in the same location as a square from the sample array. On every trial, the color wheel was presented at a random orientation and a color selector on the color wheel appeared in a random location to decrease potential for systematic response bias. Participants responded by rotating a color selector (a .36° visual angle diameter circle) both clockwise and counter clockwise on the color wheel by mouse press. Response was submitted by mouse press when the selector was at the desired response color location. The key dependent measure was the color response error calculated by subtracting the angle (on the 360° color wheel) denoting the correct color value from the angle of the chosen response color. Participants completed three blocks of this task each containing 312 trials.

**Design.** The continuous response WM task was performed under three different physical activity conditions during one session: rest, low intensity cycling, and high intensity cycling on a stationary bike. The order of these conditions was counterbalanced across participants and heart rate was required to return to within 10% of resting before each subsequent testing block. During the rest condition, participants were seated on the stationary bike in the same set up as the exercise conditions but instructed not to pedal. For the low and high intensity blocks, participants were trained to maintain a pedaling cadence of 50 revolutions per minute (RPM) by pedaling to a metronome set to 100 beats per minute (BPM). The metronome was on for the duration of the experiment, including during the rest condition. Intensity was manipulated by changing resistance; cadence was 50 RPM for both the low and high intensity conditions. The resistance level for the low intensity block was the same across all participants and produced 50 watts of power. To determine an appropriate resistance level for the high intensity block, fitness level was considered and all participants were familiarized with the Rating of Perceived Exertion (RPE) scale (RPE; Borg, 1970, 1982). RPE is a subjective rating of the intensity of physical sensations experienced during physical activity; the scale ranges from 6 (no exertion) to twenty (maximal exertion). The resistance level for the high intensity block was set such that all participants reported an RPE between 12-14. Continuous heart rate and pupil diameter measurements demonstrate the manipulation of exertion and arousal; heart rate data for one subject during the rest condition is missing due to a technical error.

**Protocol.**

***Session one.*** All participants completed the PAR-Q and were classified as eligible before completion of session one. Both sessions were completed in-lab with a researcher. During the first session, participants first provided informed consent, placed a heart rate monitor on their chest as instructed, reported previous measured resting heart rate (as instructed via email), and were weighed. Next, the participant mounted the stationary bike and settings were adjusted to accommodate their height. Participants were then introduced to the continuous response WM task and the eye-tracking component of the task. This gave the participant practice on the continuous response task (~20 trials) and allowed the researcher to ensure that the participant would eye-track well enough to complete the full experiment. Next, the participant completed the change detection WM task off of the bike. This task took about seven minutes. Finally, the participant completed the Astrand-Rhyming Submaximal Bike Test (Astrand-Rhyming, 1954).

***Session two.*** On average, participants returned for the second session within 10 days of completing the first. First, participants provided informed consent and placed a heart rate monitor on their chest as instructed. Next, participants again completed the change detection WM task. Following this, participants mounted the stationary bike and adjustments were made to accommodate their height. Participants were provided instructions to complete the continuous response task and completed ~20 practice trials after calibration of the eye tracker. The participant was then informed of the order they would complete the exercise conditions and other testing details. There was a required one-minute break every 39 trials during which the participant continued to pedal (during exercise conditions) but took a break from the computer task. Before both exercise conditions, the participant did a short five-minute warm up. Before the low intensity block this was a low-resistance warm-up that matched the low-intensity resistance level. Before the high-intensity block, this time was used to train the subject on the RPE scale and change the resistance to the appropriate level based on individual fitness level and subjective RPE. Between each block, the participant was able to dismount the bike and rest, the next block was not initiated until heart rate had returned to within 10% of resting. Upon completion of all three blocks, the participant was debriefed, compensated, and thanked for their time.

**Results**

**Physiological Measures.** Continuous heart rate obtained during the second session (see Figure 3) demonstrated a significant difference in heart rate across the exercise conditions, $F(2, 34) = 138.52$, $p < .001$. Specifically, heart rate was higher during high intensity exercise ($M = 131.50$, $SD = 15.54$) than during low intensity exercise ($M = 107.45$, $SD = 16.45$), $t(17) = -10.53$, $p < .001$. Additionally, heart rate was elevated during low intensity exercise compared to rest ($M = 79.54$, $SD = 9.85$), $t(16) = -15.43$, $p < .001$. Similarly, pupil diameter data (see Figure 4) demonstrated the expected increase in diameter as arousal increases with exercise, $F(2, 34) = 27.1$, $p < .001$. Specifically, pupil diameter was significantly larger during high intensity exercise ($M = 328.14$, $SD = 118.05$) compared to low intensity exercise ($M = 301.66$, $SD = 112.59$), $t(17) = -2.71$, $p = .015$. Further, pupil diameter was significantly larger during low intensity exercise compared to rest ($M = 265.70$, $SD = 95.87$), $t(17) = -4.14$, $p < .001$.

**Probability in Memory and Resolution.** In order to investigate how physical activity might modulate visual working memory encoding and resolution, error vectors for each subject in each exercise condition (rest, low, high) and each set size (set size three (SS3), set size six (SS6); six vectors per subject) were fit to a standard mixture model (using MemToolbox; Suchow, Brady, Fougnie, &Alvarez, 2013; memtoolbox.org). The model estimates, for each given trial, whether the tested item was likely in or out-of memory based on the degree of response error. The parameters produced by this model provide an estimate of the guess rate (proportion of out-of-memory items) and an estimate of the resolution of encoded items (represented as the standard deviation of in-memory items). The guess rate parameter was translated into a probability in memory parameter (Pmem) by subtracting the guess rate from one (1-g). In order to determine if differences in Pmem or resolution emerge across the exercise conditions, Pmem and resolution were averaged across participants within exercise conditions and within set sizes (see Figure 5).

***Probability in Memory.*** A 2 (set size: SS3 vs. SS6) x 3 (exercise condition: rest vs. low intensity vs. high intensity) repeated measures ANOVA revealed a main effect of set size on Pmem such that the probability of encoding was significantly higher for items from SS3 arrays ($M = .81$, $SD = .13$) compared to those from SS6 arrays ($M = .40$, $SD = .18$), $F(1, 17) = 249$, $p < .001$. Analyses revealed a significant interaction between exercise condition and set size on Pmem, $F(2, 34) = 4.95$, $p = .013$. Follow up tests reveal no effect of exercise on Pmem for SS3 trials, $F(2, 34) = .38$, $p = .69$. Alternately, an effect of exercise on Pmem emerged for SS6 trials, $F(2, 34) = 3.93$, $p = .029$. Specifically, Pmem was significantly lower during low intensity exercise ($M = .36$, $SD = .18$) compared to rest ($M = .43$, $SD = .18$), $t(17) = 4.45$, $p < .001$. A significant difference did not emerge between Pmem during low intensity exercise and Pmem during high intensity exercise ($M = .41$, $SD = .17$).

***Resolution.*** A 2 (set size: SS3 vs. SS6) x 3 (exercise condition: rest vs. low intensity vs. high intensity) repeated measures ANOVA revealed a main effect of set size such that resolution was better (represented by lower standard deviations) for SS3 trials ($M = 20.38$, $SD = 2.37$) compared to SS6 trials ($M = 23.83$, $SD = 6.99$), $F(1, 17) = 4.46$, $p = .049$. Standard parametric tests did not reveal an interaction or any effect of exercise condition within either SS3 or SS6 trials. This is likely due to a violation of homogeneity of variance caused by inflated variance in resolution for SS6 trials during high intensity exercise. A follow-up Wilcoxon test revealed a significant effect of exercise on resolution within SS6 trials such that resolution was better during low intensity exercise (*M* = 21.64, *SD* = 6.65) compared to high intensity exercise (*M* = 26.43, *SD* = 14.78).

**Discussion**

The current data suggest that during low intensity exercise there is a decrease in the probability that a given item is encoded paired with enhanced resolution of encoded items, specifically for supra-capacity arrays. Further, the probability that an item is encoded during high intensity exercise is the same as during rest, however, resolution during high intensity exercise seems to decrease. This pattern of data suggests the employment of a compensatory strategy during low intensity exercise such that participants selectively encode fewer items from SS6 arrays, thus decreasing Pmem and consequently enhancing resolution as more resources are devoted to fewer items.

## Study 2

To take a more critical look at the effect of exercise on encoding and maintenance, the current study employed a filtering efficiency paradigm and electroencephalography to assess whether physical activity modulated the amount of information encoded (as indexed using the CDA) and the maintenance of this information over the retention interval. It was hypothesized that the current study would replicate previous CDA findings and the amplitude of the CDA would track with the number of items encoded with a larger (more negative) amplitude corresponding to larger set sizes. Further, in keeping with previous results, it was hypothesized that subjects with low WM capacity would be less efficient at filtering irrelevant information compared to high capacity subjects. This would be evidenced by a similar CDA amplitude for trials with the same number of total items but different proportion of relevant and irrelevant items for low capacity subjects. Finally, it was hypothesized that filtering efficiency would be enhanced during exercise due to the employment of a more selective encoding strategy.

**Method**

**Participants.** Participants were 16 students from the University of California, Santa Barbara (UCSB) and 2 community members ($M_{age}$ = 20.83, $SD_{age}$ = 2.87). Participants received financial compensation for their participation ($20/hour). All participants had self-reported normal vision with no corrective lenses or contacts. Before participation, all participants completed the Physical Activity Readiness Questionnaire (PAR-Q; National Academy of Sports Medicine) to ensure eligibility to engage in aerobic activity and all participants provided informed consent. All procedures were approved by the UCSB Human Subjects Committee and the US Army Human Research Protection Office.

**Materials.** In the current study, the stationary bike and Astrand Rhyming submaximal fitness test were identical to those employed in study one.

***Change Detection Working Memory Task.*** This task was almost identical to study one, however, the large set size was reduced to six items instead of eight items. Participants completed 390 trials where 33% were set size four trials and 66% were set size six. These changes were employed after reliability testing as this version was found to have enhanced test re-test reliability compared to that used in study one. A capacity score (K) was calculated for each subject using responses to set size six trials and the equation: K = 6 * (hits – false alarms) / (1 – false alarms).

***Filtering Efficiency Working Memory Task.*** The WM task to assess filtering efficiency is a replication of current paradigms in the WM literature (Vogel, McCullough, &

Machizawa, 2005). The current study employed a gaze-contingent version in which participants fixate the center of the screen and initiate each trial by mouse press. Each trial consisted of a 100% valid left or right cue (50% right cued, 200ms) followed by a gray fixation screen (time jittered, 500ms to 1000ms), a sample array (100ms), a retention interval (900ms) and a response display (see Figure 6). The sample array consisted of either two relevant (red) rectangles (referred to as 2 item trials), four relevant rectangles (4 item trials), or two relevant and two irrelevant (blue) rectangles (2+2 item trials) with each trial type evenly presented. A full array (either 2, 4, or 2+2 items) was presented in both hemifields in order to control for the effect of visually evoked potentials. If eye position deviated >1.5° of visual angle during the presentation of the cue, jitter, sample array, or retention interval, the trial was terminated and added to the end of the block trial sequence. The rectangles in the sample and test arrays subtended 1.8° x 0.6° visual angle and were randomly presented in four possible locations within rectangular spaces 1.2° visual angle to the left and right of fixation that subtended 7.8° x 4.4° visual angle. The stimulus colors were red and blue (rgb: [1,0,0] and [0,0,1] respectively) with participants explicitly instructed to only attend to red items and ignore blue items. The response screen consisted of the same two (left and right) arrays presented in the sample array but on 50% of trials (change trials) one red item on the cued side was presented at a different orientation (change item and new orientation randomly selected). Participants responded by mouse press to report if the red items on the cued side were identical (no orientation change) to the sample array or different (at least one orientation change) from the sample array. The key behavioral dependent measure was sensitivity (d') assessed using hits and false alarms on change trials. Participants completed three blocks of this task each containing 192 trials such that all participants completed 192 trials of each trial type (2, 4, and 2+2 items).

**Design.** The behavioral task was performed under two different physical activity conditions, a within-subjects manipulation, in separate sessions: rest and low intensity cycling on a stationary bike. The order of these sessions was counterbalanced across participants. During the low intensity cycling sessions, participants were trained to maintain a pedaling cadence of 50 revolutions per minute (RPM) by pedaling to a metronome set to 100 beats per minute (BPM). During the rest condition, participants were seated on the stationary bike in the same set-up as the exercise condition but boxes were placed over the pedals and participants performed a toe-tapping task to the same cadence that pedaling in the exercise condition was performed. The metronome was on for the duration of the experiment during both sessions. The resistance level for the low intensity block was easy to maintain and the same across all participants. In order to monitor subjective exertion levels, participants were familiarized with the Rating of Perceived Exertion (RPE) scale (RPE; Borg, 1970, 1982). RPE is a subjective rating of the intensity of physical sensations experienced during physical activity and the scale ranges from six (no exertion) to twenty (maximal exertion). The WM task had built in breaks during which the participant reported RPE ($M_{RPE}$ = 9.52). Continuous heart rate measurements demonstrate the manipulation of exertion, heart rate data for one subject during the rest condition is missing due to a technical error.

**Protocol.**

***Session one.*** All participants completed the PAR-Q and were classified as eligible before completion of session one. All three sessions were completed in-lab with a researcher. During the first session, participants first provided informed consent, placed a heart rate monitor on their chest as instructed, reported previous measured resting heart rate (as instructed via email), and were weighed. Next, the participant was instructed on the filtering efficiency task and introduced to the eye-tracking component of the task to ensure ability to comply with the gaze-contingent task requirements. This also served to provide practice for the WM task (~25 trials). Next, the participant completed the change detection WM task. This task took about 30 minutes. Finally, the participant mounted the stationary bike, which was adjusted to their height, and completed the Astrand-Rhyming Submaximal Bike Test (Astrand-Rhyming, 1954).

***Sessions two and three.*** On average, participants returned for each subsequent session within one week of the previous session. Sessions two and three were identical besides the exercise condition. First, participants provided informed consent and placed a heart rate monitor on their chest as instructed. Next, EKG and HEOG (horizontal electro-oculogram) electrodes were attached to the participant and the participant was fitted with an EEG cap. Following this, participants mounted the stationary bike and adjustments were made to accommodate their height. Participants were provided instructions for the filtering efficiency task and completed 20 practice trials after calibration of the eye tracker. For the rest condition, participants were then trained to complete the toe-tapping task to the beat of the metronome. In the low intensity exercise condition, they were trained to pedal to the correct cadence. In both sessions, there was a required 30 second break every 24 trials during which the participant continued to pedal or toe-tap but took a break from the computer task. Before starting the low intensity condition, the participant did a short five-minute warm up; this was a low resistance warm-up that matched the resistance level that would be maintained for the duration of the experiment. This time was used to train the subject on the RPE scale.

The trials were split into three blocks due to the high number of trials; between each block the participant was able to dismount the bike and rest. Upon completion of session two, the participant was compensated and reminded of their appointment for session three. Upon completion of session three, the participant was debriefed, compensated, and thanked for their time.

**EEG Data Acquisition.** EEG data were recorded for each subject using an ActiCHamp system (Brain Vision LLC, Morrisville, NC) consisting of 64 active electrodes arranged in accordance with the 10-20 system in an elastic cap. The TP9 and TP10 electrodes were placed directly on the right and left mastoids. Data were sampled at 1000 Hz and referenced offline to the average mastoid signal. Additionally, electrodes were placed 1cm lateral to the left and right canthi for horizontal EOG to measure eye movement. Impedances were <20 kΩ at the start of each session.

**Data Analysis.**

***EEG Data Pre-Processing.*** MATLAB (version 2013b, The Math Works, Inc., Natick, MA) was used for EEG processing with the EEGLAB (Delorme and Makeig, 2004) toolbox. The data were high and low pass filtered at .01 Hz and 30 Hz. This low pass filter removes high frequency muscle movement artifacts (Bullock et al., 2015). The data were then epoched to -100 ms pre-stimulus onset and 1000ms post stimulus onset (100ms stimulus array and 900ms retention interval). These epoched data were then processed through artifact rejection and trials exceeding +/- 150 µV at the a priori scalp electrodes of interest (P3, P4, P5, P6, P7, P8, PO3, PO4, PO7, PO8, O1, and O2) were excluded. Finally, these data were baselined to 100ms pre-stimulus activity. In order to select the electrodes to be included for all further analyses, topographical scalp maps were produced to visually assess the lateralization of the signal during the time window of interest. For all further analyses the electrodes included were P5, P7, PO7, PO3 (left hemisphere) and P6, P8, PO4, and PO8 (right hemisphere).

In order to calculate the CDA, ipsilateral EEG activity must be subtracted from contralateral EEG activity. To do this, contralateral and ipsilateral EEG activity for each exercise condition, trial type, and cue direction was defined. Next, contralateral EEG activity for both left and right cued trials was averaged together for each exercise condition and trial type creating six contralateral waveforms per subject. Similarly, ipsilateral activity for both left and right cued trials was averaged to produced six ipsilateral waveforms per subject. Finally, ipsilateral activity was subtracted from contralateral to create a difference wave for each trial type in each exercise condition.

To determine the time window of interest, a grand average ERP waveform was created by collapsing these difference waves across exercise conditions and trial types. The peak of this waveform occurred at 463ms post stimulus onset and a 400ms time window for analysis was centered on that peak. For further analyses of the CDA, this time window (263ms-663ms post stimulus onset) was used.

## Results

**Physiological.** First, heart rate and reported BORG values were compared for the rest condition compared to the low intensity exercise condition. Heart rate was significantly higher in the low intensity exercise condition ($M$ = 109.39, $SD$ = 19.02) compared to at rest ($M$ = 76.29, $SD$ = 12.18), $t(17) = 8.61$, $p < .001$. Similarly, reported BORG values were significantly higher during low intensity exercise ($M$ = 9.48, $SD$ = 1.71) compared to rest ($M$ = 6.00, $SD$ = 0), $t(17) = 8.83$, $p < .001$. See Figures 7 and 8.

**Behavior.** Task performance was assessed using a measure of sensitivity (d'). This value, d', was calculated by subtracting the z-scored false alarm rate from the z-scored hit rate. A false alarm is when the participant incorrectly identified a trial as a change trial (detecting a change when there was not one present). Alternately, a hit is when the participant correctly identified a change trial. Performance was assessed using d' for change trials rather than general accuracy (which would also include performance on no change trials) because detecting a change is a more difficult task and, thus, d' for change trials is more sensitive than general accuracy. In order to measure the effect of capacity, a median split was performed on capacity (K) scores ($M = 3.53$, $Md = 3.74$, $SD = 1.29$) measured using the change detection task. To assess performance, a 2 (capacity: low vs. high) x 2 (exercise condition: rest vs. low) x 3 (trial type: 2 vs. 2+2 vs. 4) mixed model ANOVA was conducted on d'. First, there was no significant main effect of exercise condition such that d' during rest ($M = 3.14$, $SD = .2$) was not significantly different from that during low intensity exercise ($M = 3.20$, $SD = .22$), $F(1, 16) = .38$, $p = .55$. There was a marginally significant main effect of capacity such that low capacity subjects had a lower d' ($M = 2.77$, $SD = .29$) than high capacity subjects ($M = 3.55$, $SD = .29$, $F(1, 16) = 3.53$, $p = .078$. Further, there was a significant main effect of trial type such that a difference emerged between d' for two items ($M = 3.51$, $SD = .21$), two plus two items ($M = 3.53$, $SD = .25$) and four items ($M = 2.46$, $SD = .21$), $F(2, 32) = 42.53$, $p < .001$. Follow up *t*-tests reveal that this difference emerges due to lower sensitivity for four items compared to two, $t(17) = 8.20$, $p < .001$. There was also a significantly lower sensitivity for four items compared to two plus two items, $t(17) = 6.82$, $p < .001$. See Figure 9.

**Electrophysiology.** First, to assess the effect of capacity and exercise on CDA amplitude, a 2 (exercise condition: rest vs. low) x 2 (capacity: low vs. high) x 3 (trial type: 2 vs. 2+2 vs. 4) mixed model ANOVA was conducted. There was no effect of exercise condition on mean CDA amplitude during the time window of interest such that the CDA amplitude during rest ($M$ = -.95, $SD$ = .19) was not significantly different from that during low intensity exercise ($M$ = -.86, $SD$ = .21), $F(1, 16) = .35$, $p = .56$. There was marginally significant effect of capacity such that the mean difference wave amplitude for low capacity subjects ($M$ = -.58, $SD$ = .26) was marginally less negative than that for the high capacity ($M$ = -1.23, $SD$ = .26), $F(1, 16) = 3.13$, $p = .09$. Finally, there was a marginally significant effect of trial type such that the mean CDA amplitude for two item trials ($M$ = -1.05, $SD$ = .24), two plus two trials ($M$ = -1.03, $SD$ = .20), and four item trials ($M$ = -.63, $SD$ = .22), were not identical, $F(2, 32) = 2.87$, $p = .07$. See Figure 10.

There was an approaching marginally significant interaction between exercise and trial type, $F(32) = 2.15$, $p = .13$. Visual inspection of the CDA waveforms for each trial type during rest and low intensity exercise generated separately for low and high capacity subjects suggested that this effect might emerge solely for low capacity subjects (see Figure 11). Exploratory follow-up tests reveal that this exercise by trial type interaction does not emerge for high capacity subjects, $F(2, 16) = .13$, $p = .88$. Alternately, the exercise by trial type interaction was significant for low capacity subjects, $F(2, 16) = 10.54$, $p = .001$. Specifically, there was no effect of trial type during rest, however, an effect of trial type emerged during low intensity exercise, $F(2, 16) = 6.04$, $p = .01$. Bonferroni corrected pair-wise comparisons indicate that this effect was driven by a significantly more negative CDA amplitude for 2+2 items ($M$ = -1.13, $SD$ = .79) compared to 4 items ($M$ = .07, $SD$ = .84, $M_D$ = -1.20, $p = .022$.

## Discussion

The data reveal a significant effect of both capacity and trial type on performance. Those with low capacity had lower performance, assessed using d', compared to high capacity subjects. Performance was lower on four item trials compared to both other types. The fact that performance was the same for two plus two item trials compared to two item trials suggests that participants were able to efficiently inhibit the two irrelevant items presented in the two plus two trials. An interaction between capacity and trial type revealed that the effect of trial type was more pronounced in low capacity subjects compared to high capacity subjects. This interaction reveals that low capacity subjects showed a marked difference in performance to four item trials compared to the other two trial types, likely because the four item trials were above capacity.

Upon inspection of the CDA, the data revealed a marginally significant effect of capacity and of trial type. Low capacity subjects were found to have slightly less negative CDA waveforms compared to high capacity subjects. This matches behavioral evidence of poorer performance in low capacity subjects. The marginal effect of trial type also matches behavioral data with poorer performance on 4 item trials mirrored by less negative CDA on those 4 item trials compared to the other two. Finally, there was a moderate interaction between exercise and trial type driven by an interaction between trial type and exercise within low capacity subjects that is not present for high capacity subjects. Specifically, the CDA waves for low capacity subjects during exercise started to show greater separation in amplitude, potentially more closely mirroring the difference that we expect to see between the two and two plus two amplitudes. It is important to keep in mind that these follow up tests were exploratory tests and care should be taken when interpreting these findings.

It is also important to note that the main effect of trial type does not match previous evidence. According to prior literature, the data should show a more negative CDA for four item trials compared to two item trials (Vogel, McCullough, & Machizawa, 2005; Schwarzkopp, Mayr, & Host, 2016). The current study does not replicate this simple effect. It is possible that the requirements of the current task impacted this. During both the rest and low intensity exercise conditions, the participant was required to attend to a metronome and coordinate either toe taps (rest condition) or pedal stroke (low intensity cycling condition) to this beat. This task may have consumed WM capacity, thus preventing subjects from encoding any more information from four item trials compared to the other two trial types.

The interaction between exercise and trial type within low capacity subjects, then, may be due to different task demands during rest and low conditions. It is possible that pedaling to the cadence from the metronome consumed less WM capacity and attentional resources than performing the toe-tapping task to the same beat. Pedaling a bike is something that most participants are familiar with and it is possible that once a beat is established it is not difficult to maintain and fewer WM and attentional resources are consumed in order to maintain the beat over the course of the experiment. Toe-tapping, on the other hand, is not a natural act and it is possible that the participant had to re-attend to the metronome more often than during exercise to stay on the beat. No data was collected to assess this, however, participants did anecdotally report greater difficulty in maintaining the toe-tapping cadence compared to the pedaling cadence.

## General Discussion

The goal of the current study was to begin to explore the "online" effects of acute bouts of aerobic exercise on working memory. The general exploration of the "online" effects of exercise is critical to understand how information processing and perception may be altered by this behavioral state. Specifically, investigating what adaptive cognitive changes or detriments occur during exercise will help understand the cognitive demands experienced by individuals under physically demanding conditions such as athletes, soldiers, or any individual with a physically demanding job. An understanding of these cognitive demands and how our brain behaves during exercise will help with training and, possibly, accident prevention.

The current study focuses on working memory due to the fundamental and critical nature of this cognitive function. In order to explore the effects of exercise on WM, we have approached the question from multiple perspectives using two different tasks to try to systematically explore the facets of WM that may be affected by exercise. The goal of study one was to understand how encoding is altered during exercise from the point of view of how likely information is to "get in." Another goal of study one was to explore how resolution may be affected. If there is any degradation of resolution during exercise this is critical to know, especially when making important decisions or judgments on the basis of WM representations. The goal of study two was to take a more critical look at encoding and encoding efficiency using a neural marker (CDA) as an index of this process.

While the current data do not provide a clear answer to the question at hand, how exercise affects WM, they do provide support for the presence of some effect. First, evidence from both study one and two suggest that encoding is altered by low intensity exercise. In study one, we saw decreased likelihood of encoding coupled with increased resolution for supra-capacity trials during low intensity exercise compared to at rest, suggesting that exercise limited that participant's ability to encode up to their personal capacity limit. This could be due to a decreased WM capacity during exercise, as the result of the additional cognitive demands associated with cycling and timing (pedaling to the cadence), or the employment of a more selective encoding process. A similar, although potentially flawed, result emerged from study two, when analyzing the CDA, such that the CDA amplitude for larger set sizes was less negative than that for smaller set sizes. Specifically, the larger magnitude of this effect for low capacity subjects during exercise reflects diminished encoding either as a result of decreased capacity, excess cognitive demands imposed by pedaling requirements, or a more selective encoding process. These data should be interpreted with care, however, as we are currently unable to dissociate effects of exercise from the effects of toe-tapping and pedaling.

**Limitations**

In study two, the lack of a replication of previous CDA work suggests that an additional rest condition, without the toe-tapping requirement, should be tested to determine if the timing (toe-tapping and pedaling to the metronome) requirements do detract from WM capacity. If the lack of replication can be attributed to the additional timing demands, the effects of the current data will be more interpretable. The addition of the toe-tapping task in study two was to address concerns that the rest condition (in study 1) differed from the exercise conditions both in the physical and mental demands. In study one, the exercise conditions became dual task when the metronome and pedaling requirements were added while the rest condition did not have this timing requirement. In study two, the toe-tapping helps to correct this issue, but now, may present a new area of concern in that the cognitive demands for toe-tapping vs. pedaling may vary.

Another potential explanation for the lack of replication of previous CDA findings is that the difference between the amplitude of the CDA elicited for two compared to four items (particularly if four is supra-capacity for the participant) is not large enough to produce the classic difference in amplitude as set size increases. The CDA is believed to be an index of the number of items encoded, thus, if an individual has a WM capacity of three, this subject should encode two items from a 2-item array and three items from a 4-item array. In this example, it is easy to see that the expected increase in CDA amplitude may not be easily detectable using the 2 compared to 4-item arrays. A potential solution for this is to use 1 and 3-item arrays in the future. In this case, a 1-item array should be within capacity for all subjects and a 3-item array should be within capacity for about half of the subjects. The greater functional difference between these two array sizes may help to more clearly elicit the classic CDA effect and provide more sensitivity to assess changes in this classic pattern.

Another potential limitation is that the median capacity value for the sample in study 2 ($Md = 3.74$) is larger than that reported in previous CDA work, thus, it is difficult to generalize the current findings to low vs. high capacity individuals as the artificially created sub-groups may not truly represent a low and high capacity population. In future work it may be beneficial to obtain a sample with a larger spread of K values that is more representative.

**Future Directions**

Future investigations should aim to detangle the separate components of WM in order to determine what stage is affected by exercise. While the current data suggest that encoding may be affected, this could actually be an effect of inhibitory control or selective attention. Further, it would be interesting to investigate the effect of exercise on manipulation of information currently in WM. As discussed, work comparing older and younger adults shows a late selection compensatory mechanism in older adults that protects performance even though filtering at encoding is decreased in the older population (Schwarzkopp, Mayr, & Jost, 2016). Another potential future avenue would be to explore if exercise has a differential effects on manipulating and updating stored information after the encoding stage. While the current work does not provide a clear explanation of the effect exercise on WM it does seem to provide evidence for some effect on encoding during low intensity exercise. Future work should continue to investigate this important avenue of research to better enable us to understand the online effects of exercise on WM and information processing. This work and future findings can be applied to athletes employing WM while engaging in activity, soldiers employing WM in the field, and everyday people employing WM while moving around their environment.

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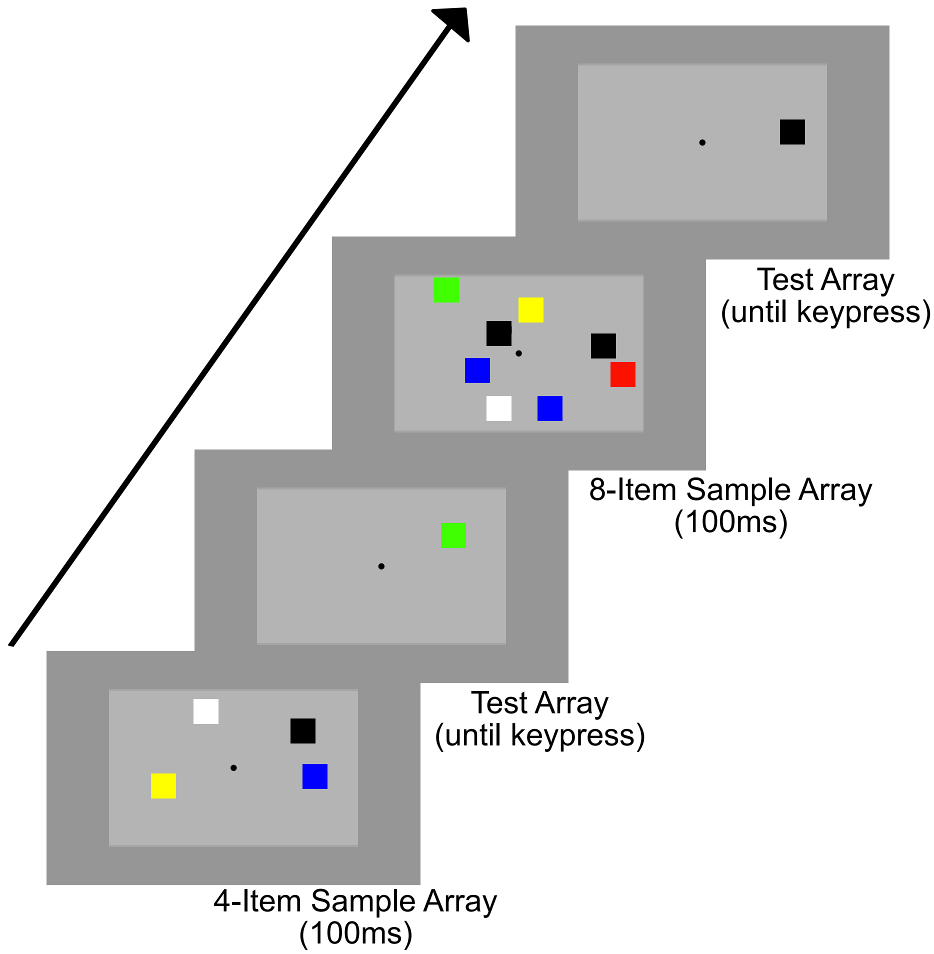


*Figure 1.* Trial sequence of change detection task. Squares in array subtend 1° visual angle, stimuli are enlarged for viewing purposes. Note that a 6-item sample array was used instead of the 8-item array for study 2.

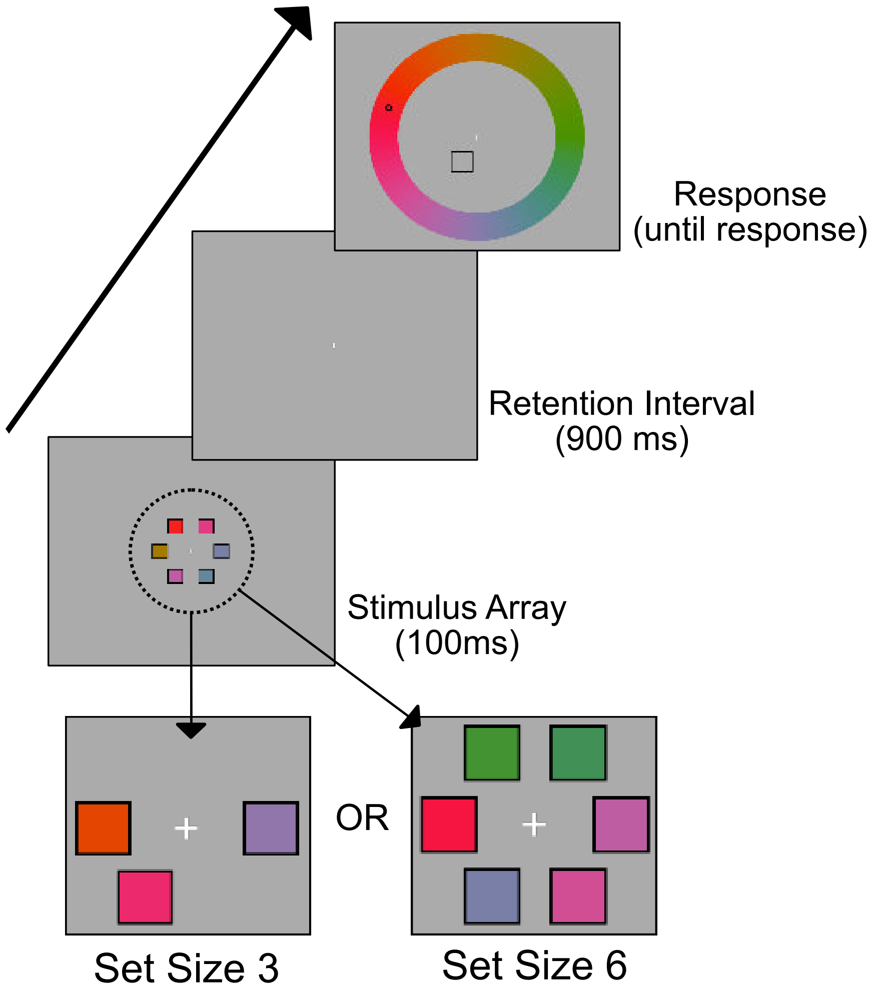


*Figure 2.* Trial sequence of continuous response working memory task. Set size randomly selected on each trial such that each block was 50% set size 3 trials and 50% set size 6 trials.

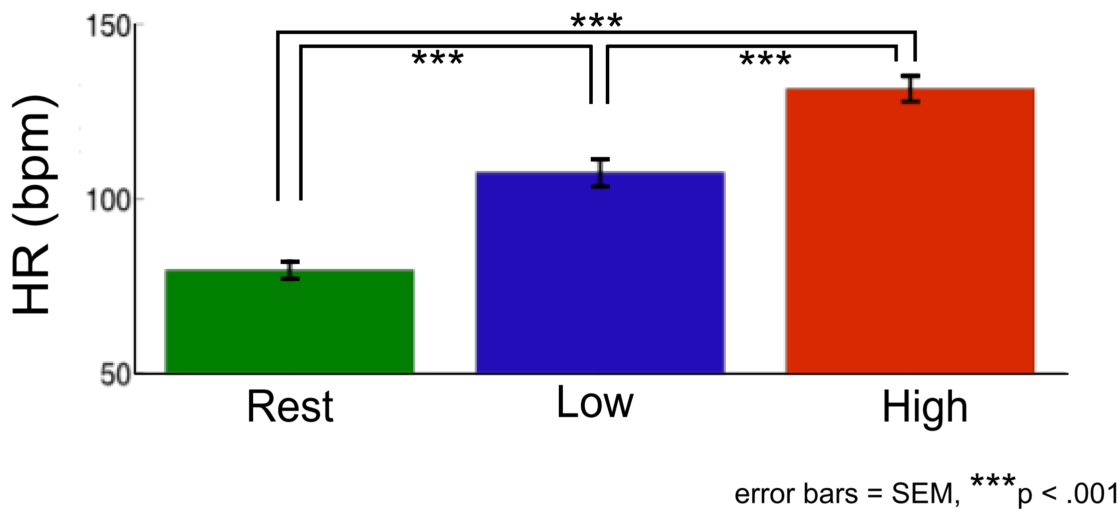


*Figure 3.* Mean heart rate across three exercise conditions.

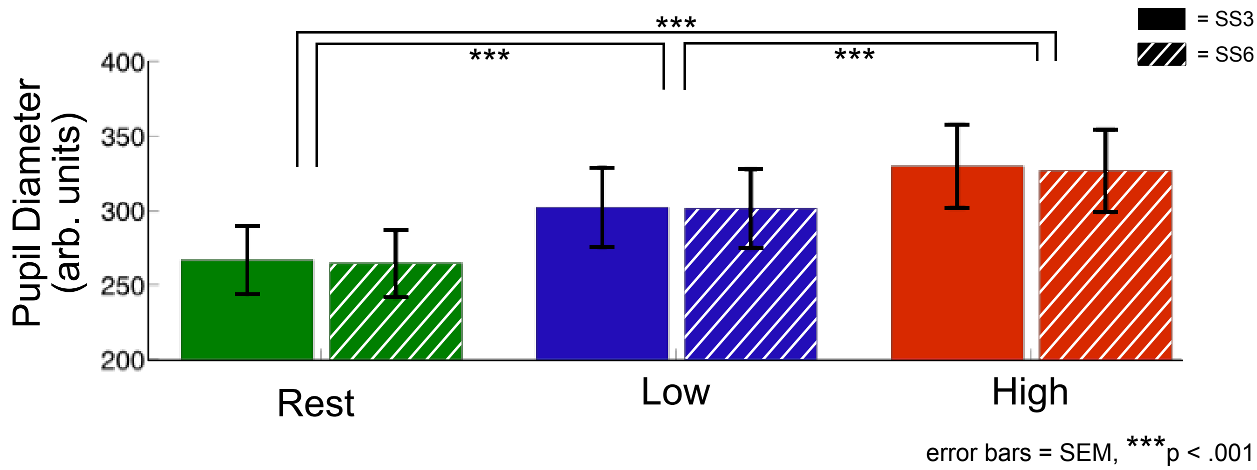


*Figure 4.* Mean pupil diameter across each exercise condition for set size 3 (within-capacity) and set size 6 (supra-capacity) trials.

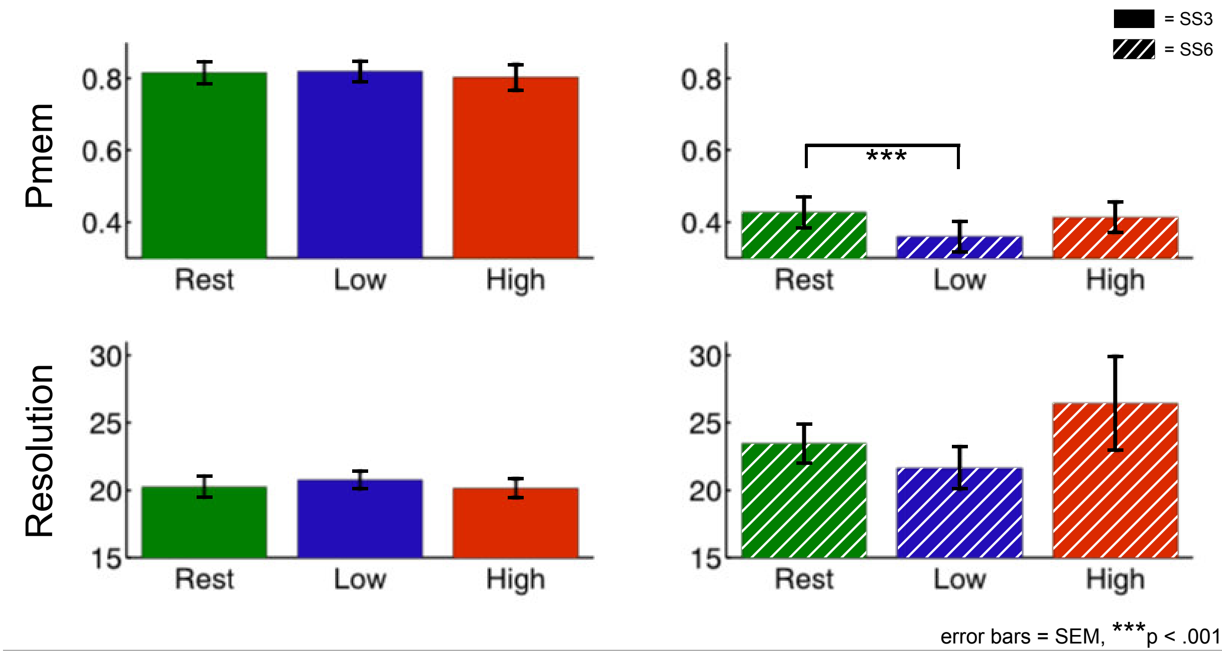


*Figure 5.* Probability in memory (Pmem) and resolution for set size 3 (solid bars) and set size 6 (striped bars) trials under each exercise condition. Pmem is significant higher at rest compared to during low intensity exercise for set size 6 trials.

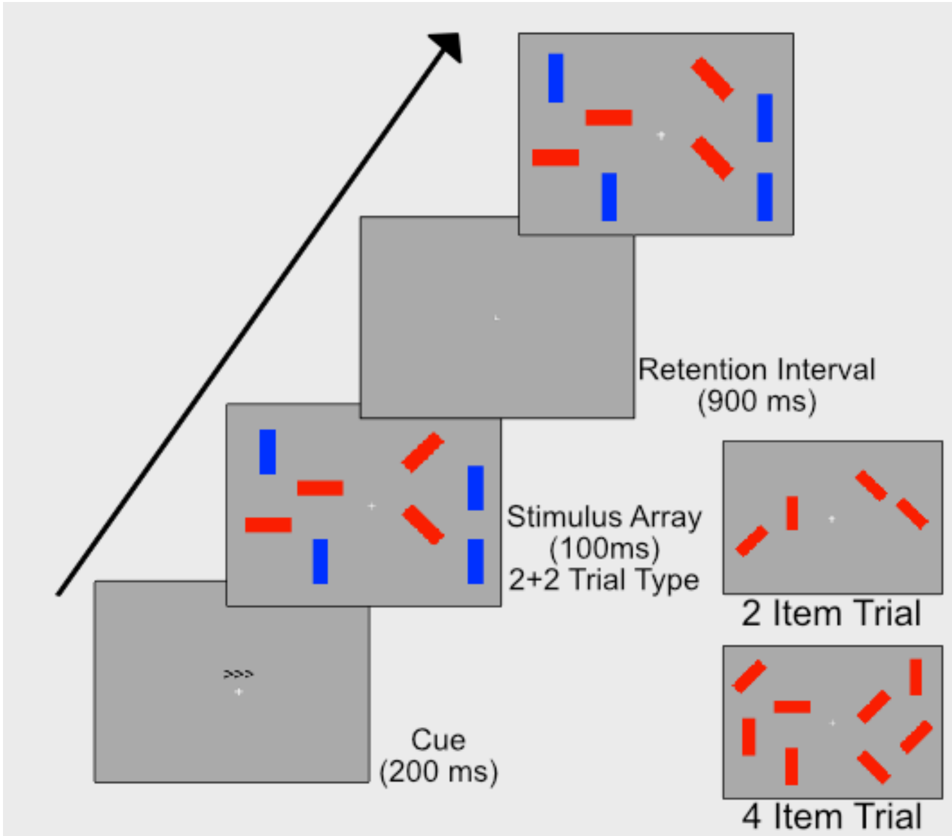


*Figure 6.* Trial sequence of filtering efficiency working memory task. Set size randomly selected on each trial such that each trial type was evenly presented in each experimental session. The location of the rectangles was randomly selected from four possible locations in each hemifield. Similarly, the orientation of the rectangles (and the new orientation on change trials) was randomly selected on every trial.

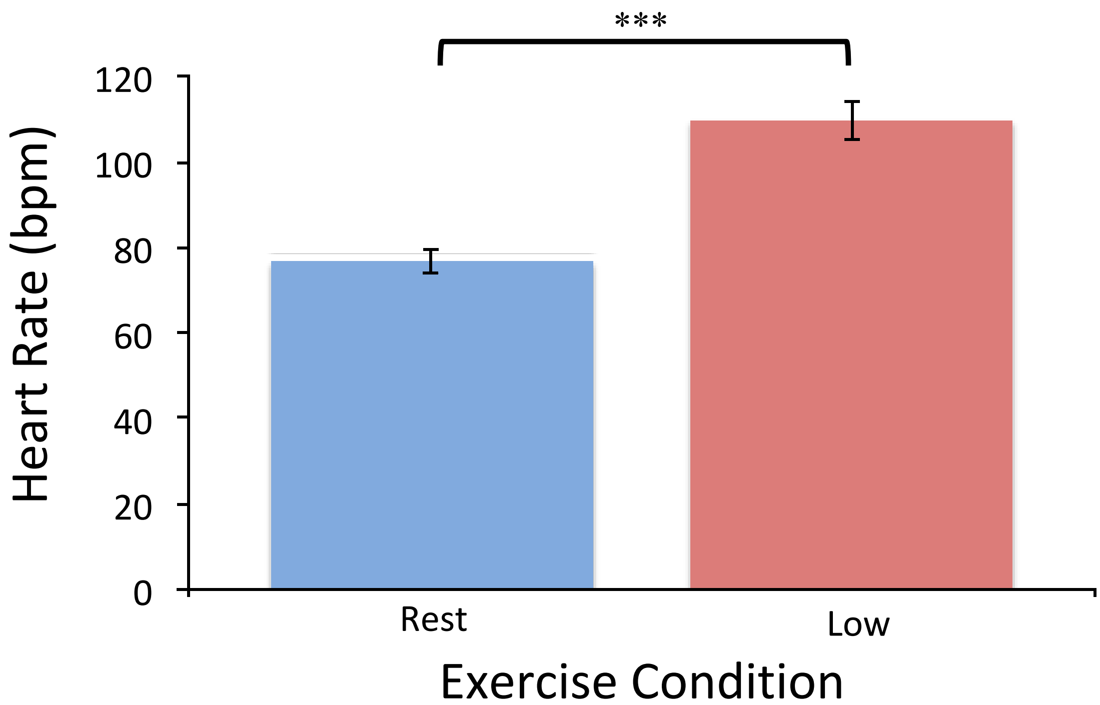


*Figure 7*. Mean heart rate across the exercise conditions. Error bars represent SEM. *** = $p < .001$.

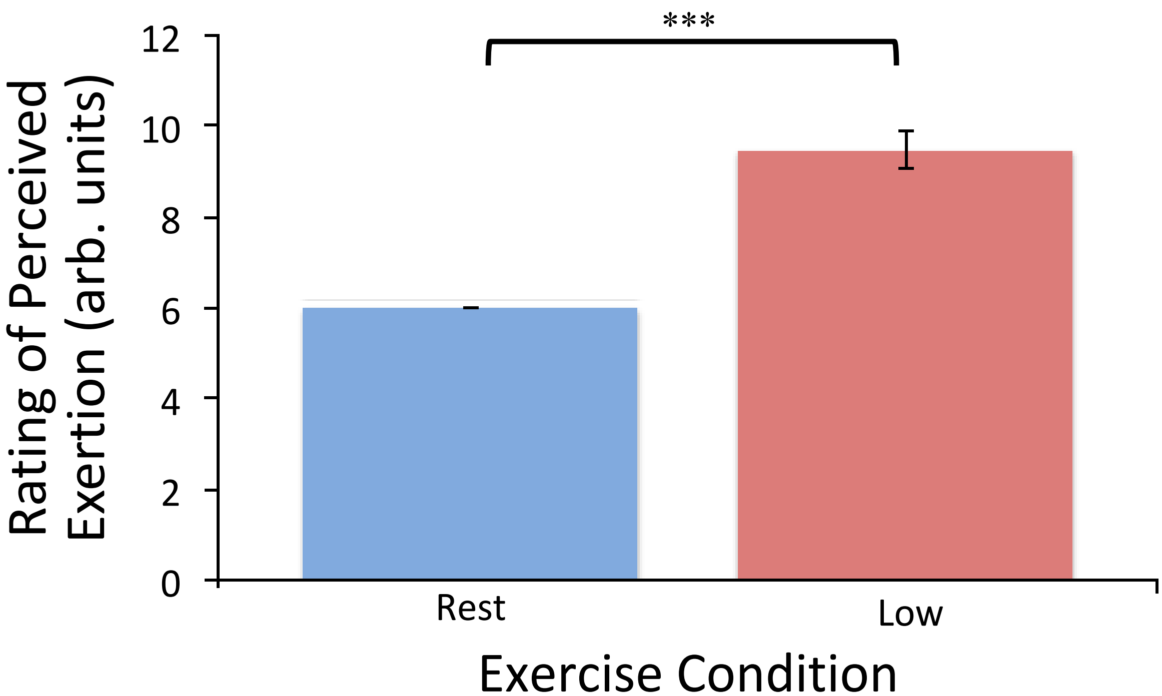


*Figure 8.* Mean BORG rating of perceived exertion across the two exercise conditions. Error bars represent SEM. *** = $p < .001$.

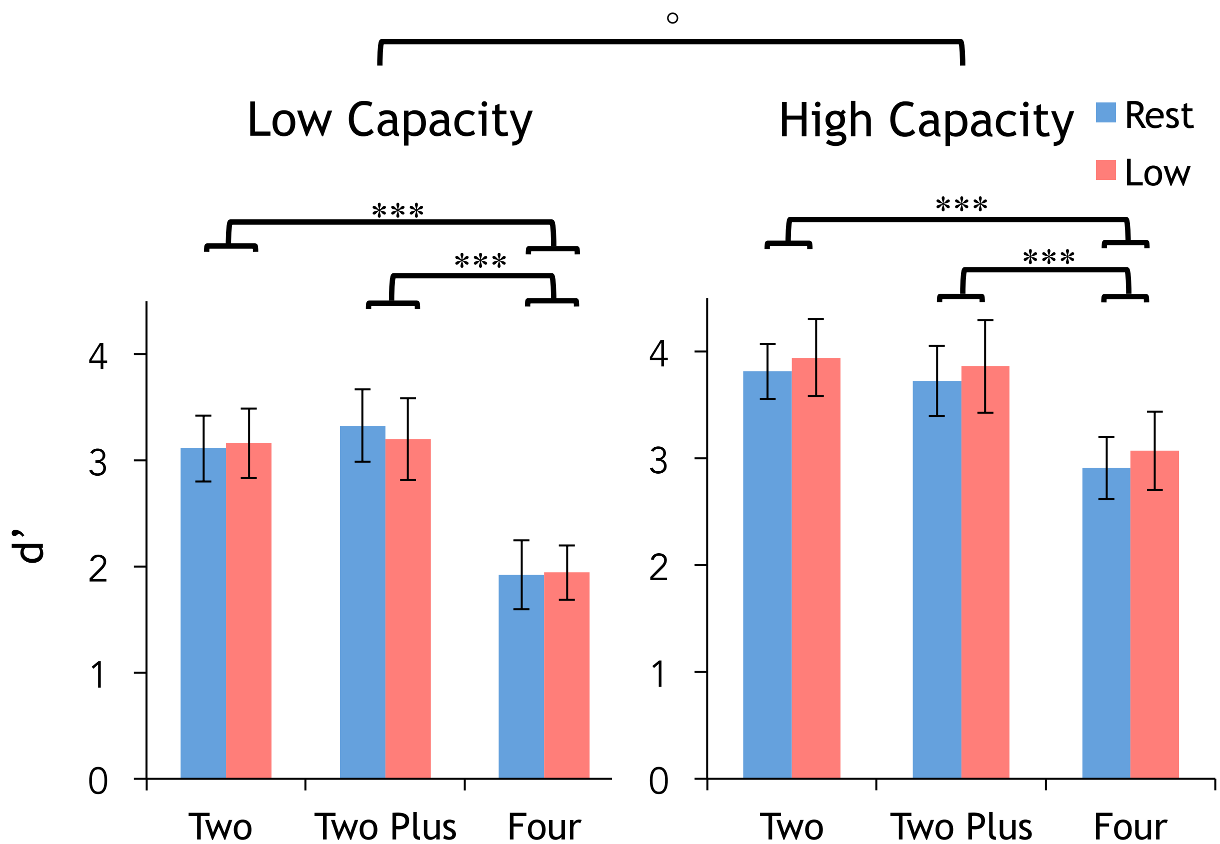


*Figure 9.* Low and high capacity subject sensitivity scores for all trial types during rest and low intensity exercise. Error bars represent SEM. ° = $p < .1$, *** = $p < .001$.

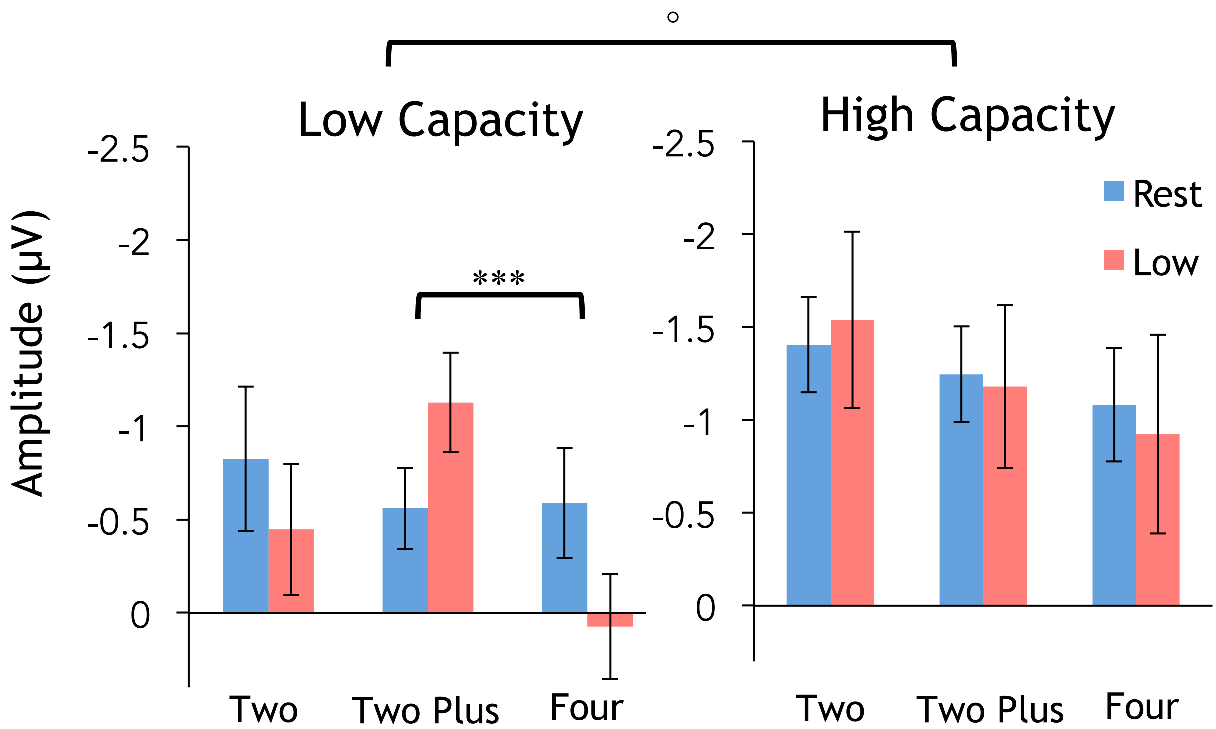


*Figure 10.* CDA amplitude over the time window of interest for low and high capacity subjects within each exercise condition and all three set sizes. Error bars represent SEM. ° = $p < .1$, *** = $p < .001$.

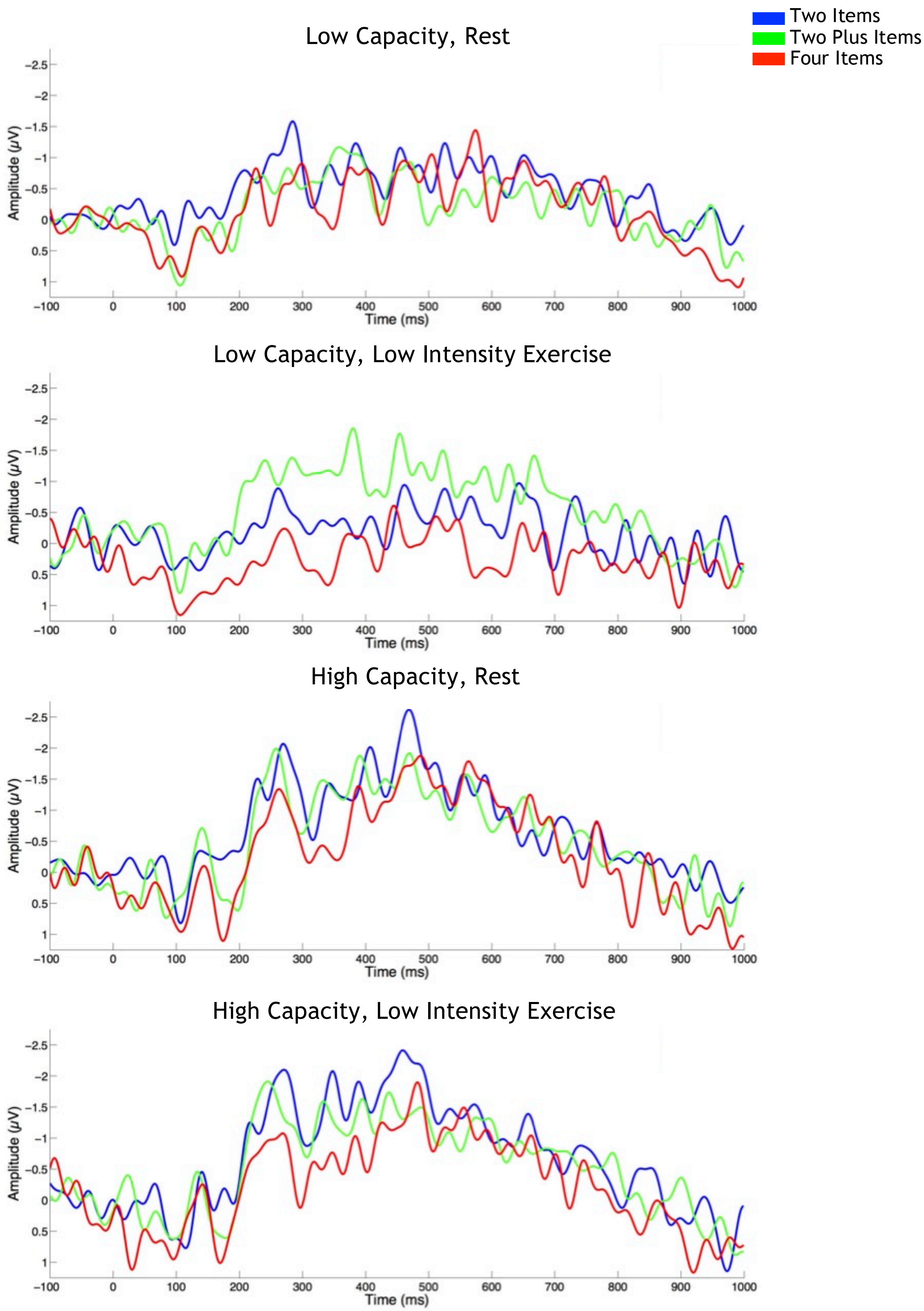


*Figure 11.* CDA waveforms for low and high capacity subjects in all exercise and set size condition.